THE NYMPHAL STAGES OF THE FIELD GRASSHOPPER, CHORTHIPPUS BRUNNEUS (THUNBERG) (ORTHOPTERA: ACRIDIDAE)

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Abstract. Hind-femora measurements of the Field Grasshopper. *Chorthippus brunneus* (Thunberg), collected at all stages of development from three sites in the Croydon area, showed that most females had five nymphal stages, while a small proportion at two of the sites passed through only four. A simple correlation found between antennal segmentation and numerical stage for nymphs of known developmental history provided an independent means of assigning a number to a nymphal stage when background details were lacking, and permitted assessment of the nymphal histories of adults. These findings are discussed against a background of the four-stage nymphal histories apparently widely found for females of this species reared in captivity.

INTRODUCTION

Captive rearing of small numbers of nymphal grasshoppers found hatching on Constitution Hill, Aberystwyth, Dyfed, in 1941, although far from successful, showed reversal of the wing-rudiments for females of *C. brunneus* occurring at the third moult, while the only female to reach the adult state passed through five nymphal stages. Similar small-scale trials at Aberystwyth in the following years on nymphs both taken in the field and hatched in captivity confirmed a five-stage nymphal development for females, as opposed to the four-stage sequence found for males of this species and for both sexes of *C. parallelus* (Zett.). Further rearing trials in 1949 on *C. brunneus* collected as first-stage nymphs from Mitcham Common, Surrey (now London Borough of Merton), led to similar results so that, although numbers involved were still low, there seemed no reason to doubt that a five-stage nymphal sequence was normal for females of this species.

The publication by Richards & Waloff (1954) of the results of their intensive study of British grasshoppers gave widespread currency to their view that both sexes of *C. brunneus* had four nymphal instars, and called into question the validity of the above conclusion. The possibility that a different developmental pattern prevailed under more natural conditions had to be considered, and a study devised that would minimise any spurious effects of captive rearing. Individual nymphs cannot readily be monitored in the field, while the statistical study of wild populations is beset with difficulties and uncertainties. The compromise adopted was to collect nymphs at all stages of development; to measure their hind-femora, count the antennal segments, note the aspect of the wing-rudiments and external female genitalia; and to retain each nymph until it had completed at least one moult, so that these features could be assessed for the next instar and thus compared with those observed in the field.

Reversal of the wing-rudiments, with the costal margins becoming directed upwards towards the mid-dorsal line and the hindwings overlapping the forewings while presenting the undersurface to the exterior, normally marks the onset of the penultimate nymphal stage (Uvarov, 1966); no exception to this was encountered in the present study. In *C. brumeus* the reversed hindwing rudiments reach to the rear end of the first abdominal tergite in the penultimate, and to the rear end of the third in the final nymphal stage. Thus for an individual having a total of N nymphal stages the last two can be recognised by this character alone and denoted as stages N-1 and N even though the numerical value of N may be unknown.

Although not forming part of the study as originally planned, a further rearing trial on nymphs hatched in captivity was undertaken to supplement the information obtained from this.

SITES STUDIED

- A. South Croydon: An area where, a few years previously, topsoil had been replaced over tipped domestic refuse, and the vegetation allowed to regenerate naturally. Here *C. brunneus* was clearly dominant, although occasional specimens of *C. parallelus* occurred, probably as vagrants from nearby established grassland.
- B. South Croydon: Disused railway sidings and adjacent abandoned allotments. C. brunneus was the only grasshopper found.
- C. Mitcham Common, London Borough of Merton: A mosaic of grassland types, where *C. parallelus* was more conspicuous than *C. brunneus*, while other species of grasshopper were also present.

EXPERIMENTAL

Site A

In 1969, 41 male and 52 female nymphs were collected, of which 22 and 31 respectively were retained for at least one moult. These were housed singly in 1-lb jam-jars, the metal closures of which were lodged in place without being screwed home. Grass cut from an untreated and unmown garden plot was supplied for food, and the jars thoroughly cleaned, every two days. The jars were kept at ambient indoor temperature, placed in the sun for an hour or so each day, but given no artificial irradiation. Humidity was probably higher than desirable, some beads of condensed moisture usually being present in the upper parts of the jars. For the final stage the nymphs were transferred singly to 2-lb jars with loose-fitting metal covers; these provided somewhat less humid conditions. All nymphal casts were retained as physical evidence of moulting.

The lengths of the hind-femora were recorded upon capture and after each moult. The insects were immobilised by being placed for a few minutes in the freezing compartment of a domestic refrigerator, and measurements made by direct comparison with a glass scale engraved in millimetres and tenths, laid above and in contact with the femur and viewed at $\times 16$ with a stereomicroscope. Measurements of hind-femora detached from nymphs that died indicated that this procedure was sound. Furthermore, measurements of the hind-femora of nymphal casts, if detached without damage to the basal end, were identical with live measurements in 67 comparisons, 0.1 mm different in 53, and 0.2 mm different in 9, the larger differences being confined to the later stages. In no instance did the discrepancy exceed 4% and occasionally a cast measurement was used when a moult occurred before a live measurement could be made.

The stage at which wing-reversal occurred was noted, and nymphs with reversed wings identified with stages N-1 or N. Some counts of antennal segments were made during life, but a much more detailed study of the antennal sheaths detached from the retained casts was made later. Many complete sequences of the latter were prepared for microscopic examination (Collins, 1988) to determine the pattern of

growth, and the agreement between their segmentation and that recorded for the corresponding live instar established. A few rough sketches were made of the developing female genitalia, but other features such as ratios of head to pronotal lengths, and details of the fastigial foveolae, tympanal grooves and wing-lobes before reversal, although changing progressively during nymphal development, proved unhelpful in the present context and were not pursued further.

Certain aspects of the results obtained in 1969 highlighted a need for further investigation and the exercise was repeated, with some modifications, in 1970. Attention was concentrated on female nymphs, 87 of which were collected and 63 retained for at least one moult. Because of the possibly adverse effects of freezing, nymphs were immobilised for measurement by gentle compression from above by the bottom of a plastic Petri dish, on which the glass scale was laid, against a film of thin rubber stretched like a drumhead over a cavity below. Provided that at least two days elapsed before moulted nymphs were thus treated, no harm resulted. As before, hind-femora measurements of nymphal casts, or of the corpses of the few that died, were occasionally used when a gap occurred in the data for live nymphs. More attention was directed to the antennae of living nymphs; counts of the flagellar segments were recorded for at least one stage of almost every individual, and confirmed for a few casts.

Sites B and C

During both 1973 and 1975 the approach of 1970 was applied to a total of 41 females from site B and 11 from site C. Counts of the antennal segments were confined to the later stages of one apparently aberrant individual from site B in 1973 and another from this site in 1975. Some sketches were made of the developing external genitalia, particularly those of the second instar.

RESULTS

Site A, 1969

The measurements of the hind femora have been plotted as histograms in Figs 1 and 2. The data for males fall into four discrete clusters, the last two of which are identified by wing character with stages N-1 and N. The progress of nymphal development is indicated by the diagonal relationship between the clusters, individuals represented in any cluster in series b to d having contributed, at one stage earlier, to the cluster one position to the left in the series immediately above. This reveals that, of 18 males taken in the first stage, 12 reached the second, 10 the third and 10 the final fourth nymphal stage. Captive rearing has had little effect on the dimensions, and the vertical correspondence between the clusters indicates that nymphs taken in the field exhibited the same four stages.

In contrast, the data for females fall into five somewhat diffuse clusters. Rearing histories showed that of the 18 nymphs taken in the first stage, two developed differently from the others, wing-reversal occurring at the second moult and full nymphal development being completed in four stages. The blocks representing these two are shown solid. A third wild nymph with hind-femora 4.1 mm long showed wing-reversal at the next moult and became adult after a further two, while two others (hind-femora 5.5 and 6.0 mm) had reversed wing-buds when captured and reached the adult state after two moults. Antennal segmentation (see below) provided strong evidence that these three were also four-stage types, and the blocks

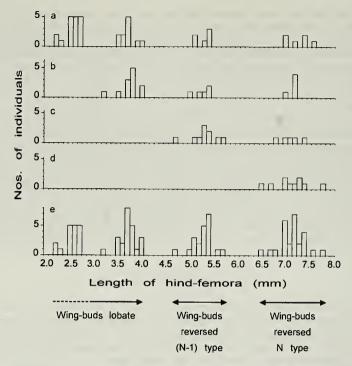


Fig. 1. *C. brunneus*. Hind-femora lengths of male nymphs, Site A, 1969: a—on capture, b—after 1, c—after 2, d—after 3 moults in captivity, e—totals of a–d combined.

displaying their development are shaded. If the contribution to the histograms of these five individuals is disregarded the clustering of the data for the remainder is much closer. The diagonal relationship already described shows that, of the 16 remaining nymphs taken in the first stage, 10 completed development in five nymphal stages, while one more may be accepted as being in this category by having N-1 type wing-buds after the third moult. Counts of the antennal segments recorded for some or all of the known nymphal stages of these 11 (Table 1) were compared with those for field specimens with incomplete rearing histories. Five individuals from the second cluster, six from the third and two from the fourth, for which this was possible, had counts that confirmed the numerical agreement between stage upon capture and position of the cluster. The predominance of a five-stage nymphal history implied by the vertical correspondence between the clusters thus received substantial independent support.

Site A, 1970

All hind femora measurements combined have been plotted as histograms in Fig. 3, where blocks representing new captures are distinguished by light shading. The pattern, as for females in 1969, is strongly suggestive of a predominantly five-stage nymphal history. A few outliers from the main clusters are again present, but none

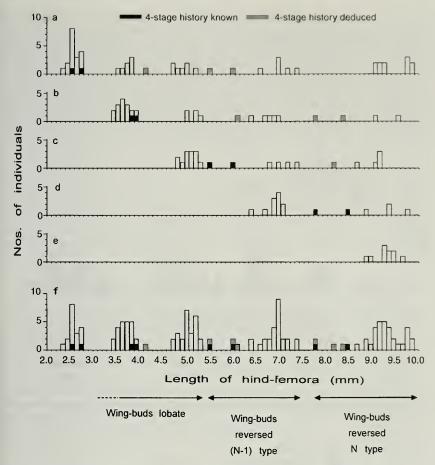


Fig. 2. *C. brunneus*. Hind-femora lengths of female nymphs, Site A, 1969: a—on capture, b—after 1, c—after 2, d—after 3, e—after 4 moults in captivity, f—totals of a–e combined.

this year could be attributed to individuals known from rearing history alone to be four-stage types. Four were however judged to be so when their antennal segmentation was taken into account; the blocks representing these are heavily shaded. These aberrant specimens would not have been recognised by hind femora length alone; only two on capture had dimensions that stand clear of the main cluster in the penultimate stage while, in the final stage, no such distinction was observed. In fact the reverse inference might be drawn, that the two individuals with hind femora 6.2 mm long in the penultimate stage, and these again plus others with hind femora of 8.9 mm or less in the final nymphal stage, could have been four-stage types. Rearing details alone were insufficient to dispel this view, but, when combined with antennal segmentation, gave clear indication of a five-stage sequence for all these.

One female taken in the first stage had wing-reversal delayed until the fourth moult and died in the fifth stage. Had it lived it presumably would have had six nymphal stages. Data for this specimen have been omitted from the results included here.

Sites B and C, 1973 and 1975

The distribution of hind-femora lengths for all stages, caught and reared, from both sites and for both years combined, are shown as histograms in Fig. 4. The close similarity of the clustering to that seen for site A indicates that again a fivestage history predominated. In 1973 two individuals from site B had hind-femora measurements that, combined with wing structure, distinguished them from the main clusters. One of these was identified as a four-stage type when the antennal segmentation was taken into account. No segmentation was recorded for the other, but the appearance of reversed wing-buds on moulting from a nymph with

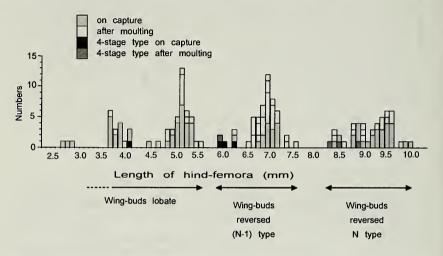


Fig. 3. C. brunneus. Hind-femora lengths of female nymphs, Site A, 1970: all data combined.

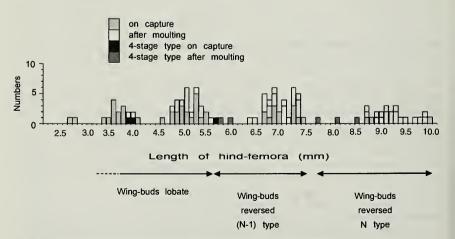


Fig. 4. C. brunneus. Hind-femora lengths of female nymphs, Sites B and C, 1973 and 1975: all data combined.

BR. J. ENT. NAT. HIST., 13: 2001

hind-femora only 3.9 mm long strongly suggested that this also was of a four-stage type. In 1975 a third specimen from site B was again regarded as having four nymphal stages on the strength of hind-femora measurements and sequence of wing development; for this the antennal segmentation provided supporting evidence. The blocks representing these three individuals are shaded more strongly.

For the second instar of most females the ovipositor valves of sternite 8 were present as a pair of blunt triangles, varying in size, but with the apices noticeably short of the rear end of sternite 9. In this they contrasted with female *C. parallelus* for which, in the second of the four-stage sequence typical of this species, the valves of sternite 8 normally reach, or even overlap, the rear end of sternite 9. Two of the nymphs apparently approached this conformation, but, for these, sternite 9 either had a strongly excised rear margin or, more probably, bore a curved pre-apical groove that could be mistaken for this; these two shared the common five-stage sequence. For the only nymph with a four-stage history to be thus examined in the second stage this feature did not appear to be markedly different from that of most of the others. It seems possible that the relative positions of these parts may change with the distension of the segments as the stage progresses and that a more extensive appraisal is needed to detect any difference, if such exists, between the two nymphal types.

Supplementary, 1976

The four-stage female taken in the second stage from site B and reared to an adult in 1975 remained in isolation until mated with a wild adult male from the same site. From the three batches of eggs laid, 17 nymphs hatched the following year. Two died at the first moult, but the remainder, housed two to a 2-lb jam-jar, were reared as described for 1969. A male and a female, both with reversed wing-rudiments, died in the third stage; 13 others reached the adult state. Of the 15 that could be categorised, five were five-stage and four were four-stage females, six were four-stage males. The antennal segmentation was recorded for the adults and for all female nymphal casts (see Tables 1 and 2), that for the four-stage females agreeing with the findings for the two sharing a known four-stage history in 1969.

Antennal segmentation

The antennae of first-stage nymphs consisted, without exception, of a scape and pedicel followed by an 11-segmented flagellum. Occasionally, towards the end of the stage, faint indications of future subdivisions became visible through the integument, but, after moulting, the flagellar sheath retained its 11 segments. In the second stage the original segmentation was still clearly defined by bold sutures, but slightly weaker new ones were visible on flagellar segments 1 and 6 and, with decreasing intensity, on segments 5, 4 and sometimes 3. Antennal casts of these and succeeding stages normally reproduced exactly the segmentation observed in the living insect. While the antennal characteristics of the first two instars offer an additional feature for identifying these, they provide no clue as to the future developmental pattern. Counts recorded here have been restricted to those for the later instars, when enumeration of the stage coupled with the aspect of the wings is of value in this connection.

The segmental counts reported by Richards & Waloff (1954) tend to span rather wide ranges, with some overlap between successive stages. Some of this variation may be attributed to the uncertain status of one of the divisions towards the base of the flagellum which, by being often weaker than the others, leaves in doubt whether the region involved should be counted as one segment showing incipient subdivision or as two segments partially fused. Mason (1954) accepted the second interpretation and appended to the total count two (or more) consecutive numbers joined by a plus sign to denote the partially fused segments; this system, with the fused segments shown in brackets, has been adopted here. Counts, expressed in this way, of flagellar segments for nymphs are shown in Table 1, and for adults in Table 2.

The differing total counts for any one of these later stages can be adjusted by the addition of the first bracketed figure. Thus flagellar counts for third instar females that, depending upon interpretation, could be regarded as ranging between 15 and 19 are brought to a common value of 22, a sum that increases by two at each subsequent moult. This regularity has been of value in deducing the numerical stage when rearing details were incomplete. In the tables, the number of individuals having any one count is indicated by two figures separated by a colon. The first of these is the number for which stage and developmental type are known from rearing history; the second is the number assigned to that stage through a shared flagellar segmentation. For the latter, inclusion in a particular developmental category has been based on a combination of numerical stage thus deduced with a rearing history that, although incomplete, includes stages N-1, N or adult.

Growth of the hind femora

The factorial increase in length of the hind-femora at each moult was calculated for the entire sequence recorded for every individual of known or deduced nymphal history. The combined values for years and sites are summarised for males and both female sequences as ranges and means \pm one standard deviation of the mean (1 sem) in Table 3. The relatively steady value of the factor over the successive nymphal

		Five-stage ♀			Four-stage ♀			Four-stage 3
		1969	1970	1976	1969	1970	1976	1969
3rd instar	16 (6+7)	0:1	0:1					
	17(5+6)	1:5	0:2	2:0				
	18(4+5)	10:5	2:9	3:0	1:2	0:1	3:0	1:1
	19(3+4)				1:1	0:3		4:9
4th instar	19(5+6)	0:1	0:1					
	20(4+5)	8:5	1:33	5:0		0:1		
	21(3+4)		0:1		0:3	0:3	3:0	4:4
5th instar	21(5+6)		0:1					
	22(4+5)	5:2	0:36	5:0				
	23(3+4)	1:0	0:1					

Table 1. Flagellar segmentation of nymphal instars.

Table 2. Flagellar segmentation of adults.

	Five-stage ♀		Four-st	Four-stage ♀				
	1970	1976	1969	1970	1973 1975	1976	Four-stage 3 1976	
$ \begin{array}{r} 23 (3+4) \\ 24 (4+5) \end{array} $	0:15	5:0	0:1	0:1	0:2	3:0	5:0	

Five-stage females, Site A, 1969-70									
Moult	lst	2nd	3rd	4th	Final				
Number	13	26	48	37	32				
Range	1.37 - 1.50	1.26 1.44	1.26-1.43	1.23-1.37	1.20-1.32				
$Mean \pm 1$ sem	1.43 ± 0.01	1.38 ± 0.01	1.36 ± 0.005	1.33 ± 0.005	1.25 ± 0.005				
Four-stage females, Site A, 1969-70, Site B, 1973, 1975									
Moult	lst	2nd	3rd	Final					
Number	2	6	11	7					
Range	1.44, 1.52	1.45-1.54	1.34-1.44	1.23 - 1.30					
$Mean \pm 1$ sem	1.48	1.49 ± 0.01	1.40 ± 0.01	1.27 ± 0.01					
Males, Site A, 1969									
Moult	lst	2nd	3rd	Final					
Number	10	15	20	12					
Range	1.37-1.54	1.38-1.47	1.26-1.40	1.20-1.27					
$Mean \pm 1$ sem	1.46 ± 0.02	1.42 ± 0.01	1.35 ± 0.01	1.25 ± 0.005					
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Table 3. Factorial increase in length of hind-femora at each moult.

stages is in accord with Dyar's rule (1890); the rather sudden decline for the final moult parallels that found for the migratory locust by Duarte (1938). The slightly larger values at each moult for the females having four nymphal stages as compared with those having five reflects the out-of-step growth patterns of the two types.

DISCUSSION

It has been shown that the majority of female *C. brunneus* studied at three sites in the Croydon area had five nymphal stages, while a small proportion from two of these passed through only four. The first intimation of a five-stage nymphal history came from the developmental pattern seen at Aberystwyth, when the possible occurrence of the shorter sequence was not foreseen. Evidence for the presence there of both types is however provided by seven pinned females, collected as adults. that remain from this period. Antennal segmentation of six confirms a history of five nymphal stages, while for the seventh it is indicative of a development completed in only four. A mainly five-stage nymphal sequence, with a small contribution from four-stage individuals, has also been reported by Hassall & Grayson (1987) for female *C. brunneus* at two sites in East Anglia. This pattern of development has therefore occurred in Britain across a wide geographical range.

Variation in instar number is well recognised in non-British Acrididae and, for some locust species, has been associated with phase variation (Uvarov, 1966). Possibly because locusts have been much studied in the swarming phase, the lower number of instars typical of this has been regarded as the norm, the solitary individuals being credited with an extra stage. Historically the term "extra" has often been applied to one particular instar, pictured as an interpolation between two consecutive stages of the shorter sequence and duplicating, in a larger version, that preceding it. Nomenclature has reflected this, so that a third instar considered as the extra has been numbered IIa. This is misleading in implying, probably incorrectly, that instar II is fully equivalent in both sequences. In the examples of female *C. brunneus* encountered here it is clear that the nymphal stages, whether four or five, follow a regular progression, with the growth of the hind-femora in reasonable agreement with Dyar's rule, a continuous development of the external genitalia and a steady increase in antennal segmentation. It is now suggested that instars would be more adequately described by a notation in which the numerical stage and developmental pattern, when known, are both shown, as in 2/4 to indicate the second in a four-stage sequence, thus emphasising the distinction between instars 2/4and 2/5. Some of these stages for female *C. brunneus* can be diagnosed with reasonable certainty although, as results for 1970 show, hind-femora measurements alone may not be sufficient. Antennal segmentation of the adults records their nymphal history and, for the last two nymphal instars, permits the identification of 3/4, 4/4, 4/5 and 5/5 individuals. Stage 3/5 may be deduced from a combination of antennal features and the possession of pre-reversal wing-buds, although there remains a remote possibility that this could be 3/6. Recognition of instar 2/4 among typical 2/5 types has not been achieved, but may come about through fuller study of the external genitalia. No means of distinguishing between instars 1/4 and 1/5 have been found, if indeed the future developmental route is already predetermined at hatching.

There remains the question of the significance of the naturally-occurring fourstage females and the factors influencing their production. Any effect comparable with phase variation would require the four-stagers to be more frequent in dense populations, or, at least, among the offspring of such populations (Albrecht, 1955). No attempt was made to assess the population densities of the colonies studied here, but the low incidence of four-stagers would not have permitted valid comparison. For non-British grasshoppers, variable instar numbers have been associated with temperature (Parker, 1930), geographical range (Shotwell, 1941) and food (Smith, 1959). Several workers since Richards & Waloff, rearing females of C. brunneus in captivity, have clearly indicated a four-stage nymphal development (Moriarty, 1969), strongly implied this (Kelly-Stebbings & Hewitt, 1972) or at all events made no comment contrary to the prevailing view, so that Hassall & Grayson (1987) regarded their finding of five stages as abnormal. It is difficult to assign common features to accounts of captive rearing, but fairly widely reported are an elevated laboratory temperature, artificial irradiation, grass specially grown for food, rearing in groups and housing in better ventilated conditions than those described here. Sometimes the specimens have been drawn from stock maintained in captivity for several generations. Hassall & Grayson (1987) found that second-generation laboratorybred females from one site passed through only four nymphal stages when the quality of their food was reduced.

Such factors may not be the only influence, as both types of female were among the siblings hatched in 1976 and reared under similar conditions; indeed one of each type actually occupied the same jar throughout nymphal development. That these were the offspring of a four-stage female might suggest a heritable effect, although whether truly genetic or more akin to the transmission through the generations of phase differences cannot be determined on this evidence alone. Whatever may be the explanation for the presence of four-stage females in natural populations it would seem that this is most likely to be provided by those encountering them routinely during captive rearing.

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SHORT COMMUNICATION

Stignus pendulus (Panzer) (Hymenoptera: Sphecidae) associated with ancient woodlands in south-east London.—Since Stignuus pendulus was first discovered in Britain by Allen (1987) it has remained rather a mystery. At the time of Falk's review (1991) it was known only from Allen's original East Kent specimen and two more from the other side of the Thames in South Essex. Published records seem few: Uffen (1997, 1998) has recorded it twice from Hertfordshire. However, it is obviously much more widespread and there are many more records from South Essex (P. R. Harvey, personal communication) and Surrey (Baldock, in preparation). I was not, therefore, too surprised to find it at several localities in the London area.

What I did find surprising, or at least ironic, is that here it seems to be associated with ancient woodland! So far *Stignus pendulus* has been found at four sites.

Sydenham Hill Woods, Dulwich (TQ3472, Surrey), 20.vi.1993, 30.viii.1993, found by D. W. Baldock in 1997 in Malaise trap material which had been stored in alcohol for several years. Sydenham Hill and Dulwich Woods are reckoned to be remains of the "Great North Wood", a series of oak copses and wooded commons extending through south-east London from Selhurst to Brockley. A large number of